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ALTERNATIVE INTERPRETATIONS FOR THE EVIDENCE THAT CERTAIN ORCHIDS AND BROMELIADS ACT AS SHOOT PARASITES

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INTRODUCTION

Recently I proposed that epiphytes should be considered "nutritional pirates" rather than either parasites or conventional competitors for minerals with the trees they occupy. A pejorative label seems to be appropriate for these organisms in light of the nutritional hardship one study suggests that they can impose on a host (Benzing & Seeman, 1978). The impact epiphytic plants have on their supports as nutritional pirates is influenced by many factors. Some are related to the nature of the epiphyte involved and its position in a host crown. Local edaphic conditions are also influential.

Epiphytes located at the top of the forest profile mostly absorb mineral salts dissolved in precipitation and washed from wind-borne particulates lodged on their surfaces. Within the crowns of living trees, however, an epiflora also accumulates mineral nutrients that previously served the host. Prior to their co-optation by an epiphyte, these minerals were either leached from adjacent vegetation by rainfall, or, in the special case of the tank bromeliads, were released from decaying host litter trapped in foliar impoundments. Nutrients fluxing in litter and leachates from a crown free of epiphytes can be recycled by the tree that lost them.

A tree growing on a fertile site can lose proportionally little of the mineral material cycling between its shoot and the substratum to an epiphyte load. Hence hosts with access to excess nutrients should exhibit no ill effects specifically attributable to the nutrition of the epiphytes in their crowns. Conversely, on soils where the scarcity of at least one mineral element is sufficient to limit plant growth, or where the supply is close to that point, a tree's vigor may exhibit an inverse relationship to the success achieved by an associated population of epiphytes in garnering that same substance. Epiphytes grow sluggishly and produce little litter. Nutrients sequestered in their bodies are effectively removed from circulation for long periods and remain unavailable for reuse by the host over those intervals. Inputs to the ecosystem from the atmosphere or parent material are apt to be too small to compensate for the effects of extensive pirating on very infertile sites.

In extreme circumstances, the impact of a sufficiently developed colony of epiphytes could increase until a point is reached where the leaf area index of an infested tree begins to decline. As this value diminishes crown transparency could become high enough to encourage even heavier exploitation by shade-intolerant, oligotrophic epiphytes, further exacerbating the deprivation of the host. In essence, once the effect of an epiphyte load exceeds some threshold level, a feedback mechanism may become operative. If and when this happens, the condition of the tree — its vigor and general health — would deteriorate further.

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THE EFFECTS OF EPIPHYTES ON NONSTRESSED HOSTS

Nutritional piracy was offered to explain a particular phenomenon: why some trees on infertile substrata become progressively pauperized as their epiphyte loads expand. As intuitively appealing as this hypothesis may be, it cannot be used to refute all the cases made so far in support of the notion that some epiphytes are, in fact, acting as direct parasites or epiparasites. Two authors have reported incidents of suspected parasitism by orchids involving citrus, coffee, and other cultivated vegetation (Ruinen, 1953; Johansson, 1977). Nuernbergk (1974) concurs with Ruinen's thesis that some epiphytic orchids can be epiparasitic on their hosts. Parasitism was invoked as the possible cause of damage to *Terminalia mollis* Laws. in West Africa by Johansson because its orchid epiphytes were more abundant on dead and moribund branches than on live ones. Site quality was not discussed in either of these publications, but since some of the affected trees were orchard crops or arboretum plantings, I assume that at least a few were growing on relatively fertile soil. In any case, the symptoms described are not those expected where piracy is the causal factor. Nutritional piracy should produce a general pauperization, not the localized damage reported by Johansson (1977).

Dismissing the effects of shading, girdling (Cook, 1926), and the possibility of parasitism for the moment, how else could an epiphyte adversely affect its host on a fertile site? Perhaps another question is more to the point. If these plants are not damaging a particular support, why are they so often associated with dead or dying branch complexes? A plausible explanation for this association may be found by considering the ontogeny of affected hosts and their architectural models.

THE ONTOGENY OF WOODY PLANTS

Although usually long-lived and relatively large at maturity, trees, more than many herbs, exhibit determinate growth. During a lifetime most trees produce a massive shoot built around just one major axis. Within limits, this shoot complex passes through a series of inherently programmed developmental stages. The longevity of a particular stem axis within the crown of a tree relative to the life span of the whole organism is determined by (a) its place in space and time within the sequence of ontogenetic events that transpire during the development of a particular specimen, (b) the model characteristics of the species involved (Hallé et al., 1978), and (c) local environmental factors that affect the ability of a specific tree to conform to its architectural model and maintain a healthy crown.

So far 23 models have been described to categorize the architecture of arborescent plants (Hallé et al., 1978). Specific architectural models are adaptive and confer fitness under certain environmental circumstances. Some models program for a crown structured to display its photosynthetic surfaces as a monolayer, others as a multilayer (Horn, 1971). When vigor is high, certain models promote the development of a dense crown — one that casts deep shade. Transparency is always high in other cases. Leaf shape, size and orientation, all of which influence crown opacity, may also be correlated with particular models.

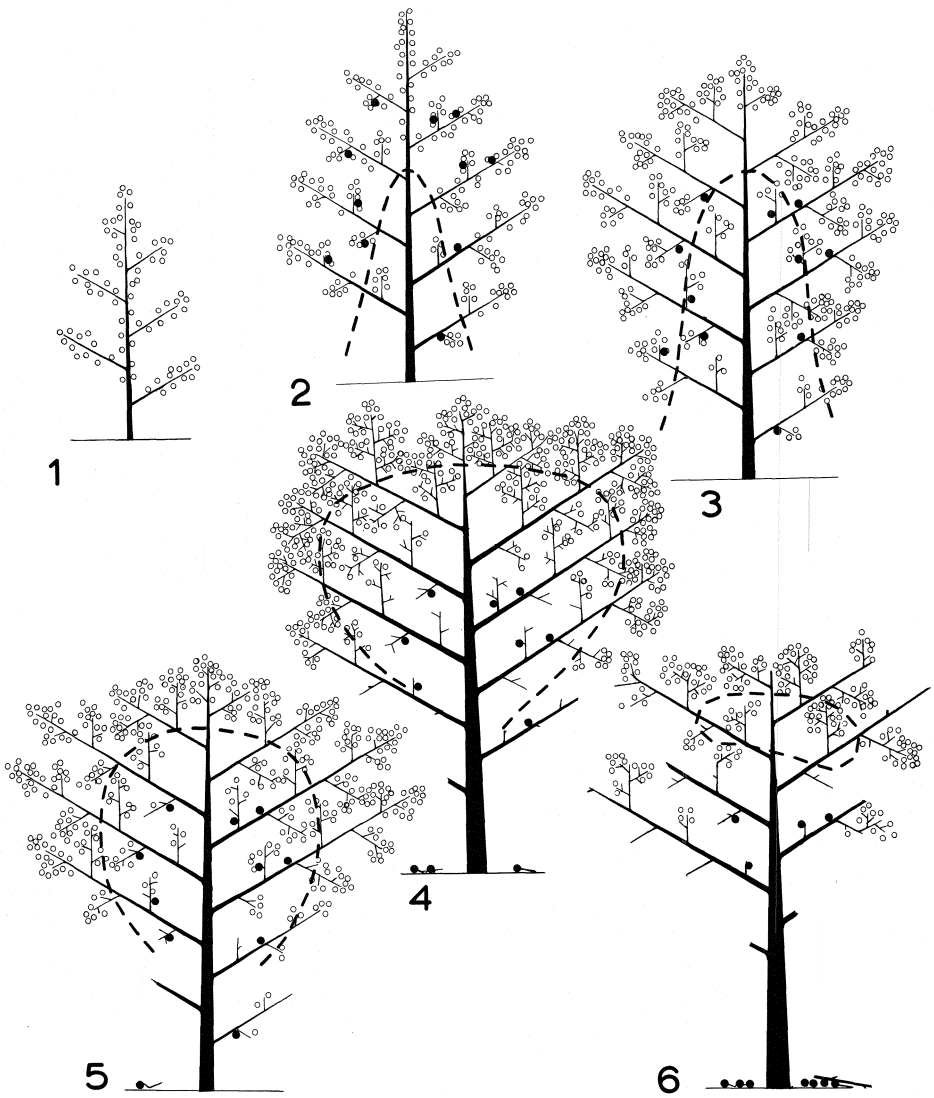
Trees on moist, fertile sites, unshaded by neighbors and free of major mechanical or biological disturbance, express their architectural model more

fully than those that occur in dense stands or on locations where edaphic restraints limit vigor. Severely disadvantaged specimens exhibit limited or opportunistic growth which leads to distorted or pauperized expressions of their architectural model.

Broadleaf trees usually conform to complex architectural models. During their ontogeny, most individuals proceed through a series of developmental stages beginning early in the juvenile phase with the formation of a number of potentially long-lived primary lateral axes (Fig. 1, 2). This first order of divisions results in a model-specific branching pattern. Some years later, all or most of the lowest branch complexes have died and fallen away (Fig. 4). By that time each of the remaining laterals located above them, where sufficient light has been available, have proliferated a second time in a pattern faithful to the initial one (Fig. 2). Second order axes undergo a third reiteration and so on as the crown rapidly expands (Fig. 3-5). Repeated reiterations, usually no more than five or six in all, eventually yield a sequence of progressively smaller branch complexes all of which conform to the same model-specific architecture. Successive reiterations are not only progressively miniaturized, but the growth potential of each of their constituent axes is further restricted. Finally the periphery of the crown, where most of the remaining active shoot meristems are located, approaches a maximum dimension and achieves a kind of dynamic equilibrium (Hallé et al., 1978). Diminutions of growth potential that accompany each successive reiteration are enforced by functional limitations inherent to certain size-form relationships that affect the shoots of all arborescent plants (Zimmerman & Brown, 1971).

Over a number of seasons, the terminal meristems located at the stabilized periphery of the crown of a fully mature tree elongate slowly while generating ephemeral organs (leaves and fruiting structures) in a fashion not unlike the production of annual shoots by the perennial axes of many rhizomatous temperate herbs. Ultimately each terminal axis declines and its meristem dies. For a time, similarly proportioned and growth-constrained branchlets are generated to replace those lost through normal attrition, and the overall dimensions of the crown remain static (Fig. 5). At some point, the tree as a whole starts to decline (Fig. 6). This begins when new meristems are no longer produced at a rate sufficient to replace all of those that die. As replacement falls off, the crown thins until entire major branch complexes fail. The organism finally succumbs or, in its weakened condition, is toppled by wind or killed by pathogens or predators.

Considered in this perspective, the tree, by virtue of its extended ontogeny and overall organization of parts, emerges as a system of axes of limited growth potential and life span. These axes are grouped into temporally and spatially distinct, and successive but overlapping, populations. Only the major axes of a tree — the trunk and some of the main lateral stems — remain viable for more than a small fraction of the existence of the whole organism. Branch complexes and their individual components survive only as long as they remain nutritionally self-sufficient. Death ensues once the exposure of a particular complex or an individual axis is reduced below its light compensation point by the overgrowth of adjacent vegetation. That overgrowth may be affected by other parts of the same tree or by nearby competitors. Because of progressive shading as well as other factors, the service life of a particular bark surface for an epiphyte is likely to be even shorter than the duration of the axis itself and much less than that of the whole tree.



Figures 1-6. The ontogeny and decline of a hypothetical host for a heliophilic vascular epiphyte. The dark circle represents epiphytes that colonized axes in the crown while the tree was a juvenile. The dotted lines delimit that part of the crown center where shading has reduced illumination below the light compensation point for shoots of the host species. Note that by the time the host is mature, most of the epiphytes are anchored to dead members of the crown. Many of these have fallen to the ground by the time the tree completes its life cycle.

TAXODIUM ASCENDENS AND ITS EPIPHYTES IN SOUTHERN FLORIDA

Taxodium ascendens Brongn. illustrates the concept of the architectural model particularly well as it bears on the suitability of a tree as a host for a typical angiospermous epiphyte, a slow-growing plant with a requirement for moderate to high exposure. This conifer, like a number of others, conforms most closely to Rauh's model (Hallé et al., 1978). When cypress develops on moist, fertile, open sites — i.e., when the model can be expressed fully, its trunk is monopodial and orthotropic (Fig. 7). Successive tiers of less robust, plagiotropic lateral branch complexes form and all but the very lowest persist through maturity to contribute to a pyramidal crown. Vigorous crowns expand rapidly and are relatively opaque compared to those of dwarfed individuals growing on less favorable sites (Fig. 8).

Only a small fraction of the numerous lateral branch complexes that could be present and viable at maturity branch extensively and persist in older, stressed specimens growing on the shallow, relatively sterile soils underlying much of Collier and Monroe Counties in southern Florida (Fig. 8). Early in the developmental sequence these individuals become dwarfed and remain low and open thereafter. Fire and wind damage may occasionally further alter the course of growth. For a time a replacement, supported by an established root system, may expand vigorously and closely conform to the model. Eventually vigor diminishes, many young lateral branches die, and the new crown or new sector in the original crown assumes the usual pauperated form.

Much of the surviving bark surface on a mature dwarfed pond cypress has been exposed to strong illumination from inception and will continue to be so for the remainder of the life of the tree. As a result, these pauperated individuals can host unusually long-lived specimens of the common butterfly orchid *Encyclia tampensis* (Lindl.) Small and several heliophilic tillandsias. *Tillandsia balbisiana* Schult., *T. circinnata* Schlecht. and *T. fasciculata* Sw., all relatively shade-intolerant species are nowhere more common as older adults in southern Florida than on the dwarfed cypress trees of the Big Cypress Swamp.

Cypress is not nearly as suitable for the same epiphytes when growth is less restricted and the model is more fully expressed. Vigorous trees in southern Florida support far fewer high exposure epiphytes, probably because their bark surfaces become heavily shaded too quickly or expand too rapidly to provide suitably illuminated or stable sites with a long enough term of service for these slow-growing plants.

THE ASSOCIATION OF MATURE EPIPHYTES AND DEAD AXES

If a particular branch, regardless of its location in the crown, occupies an exposed position longer than others of comparable age, that member of the crown will not be self-pruned as quickly as other more heavily shaded axes produced during the same developmental stage (reiteration). A branch with an unusually extended history of exposure is likely to die or become a moribund relic well after comparably aged parts of the crown fall away at the end of the normal life span for members of their "ontogenetic category." The more extended its "place in the sun," the more likely that a branch will be successfully colonized by epiphytes and the larger (older)

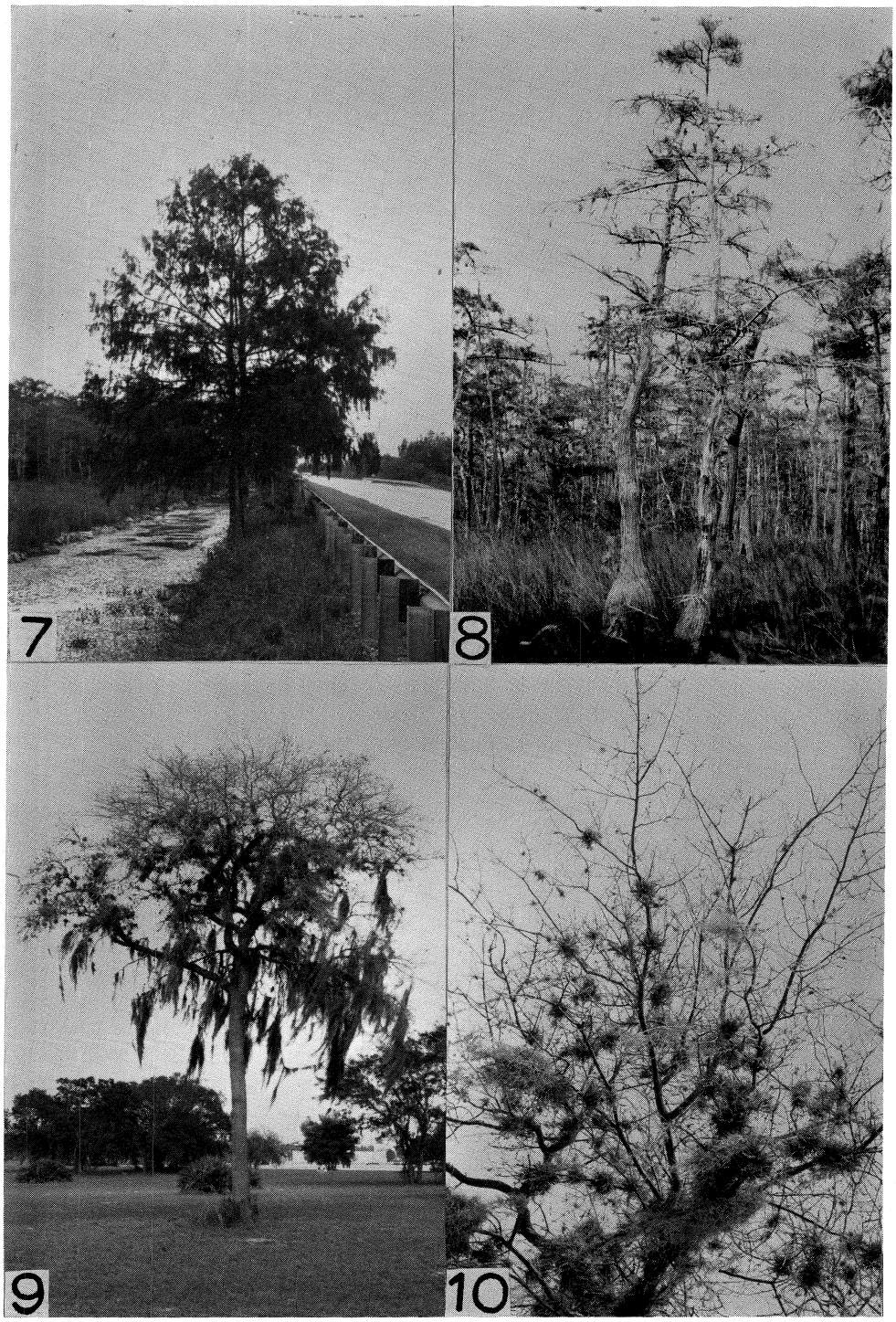
those plants will grow before being shed or suppressed by heavy shade. In effect, the longer an axis remains exposed, the more likely the epiphytes located there will eventually appear to be responsible for its death.

Most of the dead and weak axes routinely found in the canopies of woody species, especially the healthiest members of those populations, were neither prematurely killed by outside agents nor did they live an extended life because of an unusually prolonged term of exposure. They were simply destined by the normal growth processes characteristic of a particular architectural model to have relatively short lives. To an observer unaware of the place of a dead or moribund branch in the ontogenetic process or of historical events that may have lengthened its life, the presence of an unusually large number of well-developed epiphytes there suggests that these plants are responsible for the condition of that axis.

Neither the exact exposure preferences nor the life histories of epiphytes so far identified as suspected parasites are known. Most assuredly, all of these organisms require several years to become large reproducing specimens. Assuming that these species are at least moderately intolerant of shade and rain shadows cast by heavy foliage, and that individual plants require an extended period of growth to become robust older adults, the highest densities of large specimens would be expected on the oldest surfaces or those that have been exposed to strong illumination the longest. Younger substrata, or those axes present within the more fully foliated parts of the host crown, are likely to be too new or were too quickly heavily shadowed to have nurtured comparable densities of equally mature and vigorous epiphytes. Clearly the disproportionately high incidence of epiphytes on dead and dying branches cannot be construed as a priori evidence that the former are parasitic or that they have had any particular effect on a host. Equally plausible, and in fact more likely, is the possibility that this association occurs because most of the axes involved are the oldest, or have experienced the longest terms of exposure in the crown.

A thorough test of the hypothesis that spatial and temporal factors rather than parasitism are responsible for the high incidence of mature epiphytes on dead portions of a host will be difficult to accomplish. Any systematic attempt to explore the epiphyte-host relationship from this perspective will require that the investigator have a means of determining the ages of large and small axes, both living and dead, and of the epiphytes secured to them. This will not be an easy task. Older epiphytes may defy dating. Without growth rings, tropical trees represent a similar problem to the dendrochronologist. Should these limitations be overcome, however, and a thorough knowledge of the architectural model and the ontogeny of the hosts in question be achieved, surveys can be made to determine the age-specific distribution of epiphytes relative to the age and the exposure histories of the axes they occupy.

Figure 7. A vigorous young adult specimen of *Taxodium ascendens* growing on an open fertile site where its architectural model has been expressed fully.
Figure 8. Dwarfed adult specimens of *Taxodium ascendens* growing on infertile shallow soil in Collier County, Florida. The architectural model of these specimens is severely pauperated.
Figure 9. A moderately vigorous young adult specimen of *Quericus virginiana* in the leafless condition supporting the epiphytes *Tillandsia recurvata* and *T. usneoides* in Collier County, Florida.
Figure 10. A single leafless branch of a vigorous young adult *Quercus virginiana* specimen. Note that the *Tillandsia recurvata* specimens located there have become progressively larger as they were displaced deeper into the canopy by crown expansion.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PRELIMINARY EVIDENCE

A cursory examination of *Tillandsia recurvata* L. on live oaks in southern Florida, where as an adult it is routinely congregated on dead twigs, suggests that a more extensive analysis may provide support for the hypothesis that at least this epiphyte does not directly harm a host. *Quercus virginiana* Mill. like *Taxodium ascendens* conforms to Rauh's architectural model (Hallé et al., 1978) and produces monopodal trunks supporting many tiers of plagiotropic axes (Fig. 9). These lateral branches reiterate several times by generating numerous proleptic branch systems in several orders, each comprised of stems of decreasing length and diameter. The higher order, slow-growing laterals generally die within a few years as they become heavily shaded by extension and further branching of their own and adjacent branch complexes (Fig. 1-6). The relative age of these twigs in the higher order complexes can be estimated by position. The oldest ultimate twigs in a particular lateral branch system—those initiated early in the ontogeny of that complex—are located proximal to and often below the bulk of the viable twigs in that same complex. It was on these older, relatively short-lived branchlets that I encountered approximately 80% of the mature *T. recurvata* growing in the middle to lower portions of the canopies of ten mature live oaks. The remaining fruiting specimens were secured to the main trunk and the more permanent larger and longer-lived axes of the lateral branch complexes. Of 95 fruiting specimens secured to small twigs throughout the lower and middle canopy, 70.5 % were anchored to dead axes. Numerous adjacent stems of apparent similar age and about the same size but harboring no mature ball moss specimens were also lifeless. Juveniles were very common on dead and living stems.

These observations strongly suggest that the supports bearing the bulk of the oldest *T. recurvata* specimens in the lower crown of the oaks examined were destined to die after a relatively short life whether an epiphyte was present or not. Such a finding is not unexpected since most of the serviceable surfaces exposed to wind-blown seeds at any point in life are located at the periphery of a live oak canopy and belong to the very numerous small stems programmed by its developmental process to have brief lives. Given the five or more years required by *T. recurvata* to fruit for the first time, the high incidence of mature specimens, most of which had already fruited several times, on dead or moribund axes deeper in the canopy is not likely to be either coincidental or reflective of the nutrition of the bromeliad. The displacement of small lateral axes with a predetermined limited growth potential well into the canopy — an event that ensured them a short life — took place while the attached epiphytes were becoming older fruiting individuals (Fig. 10). Figures 1-6 summarize the growth processes of a hypothetical host that progressively displaces epiphytes deeper into its canopy, thus increasing the probability that the oldest orchids or bromeliads encountered in that crown will be residing on dead axes.

ARE "SHOOTLESS" ORCHIDS PARASITES?

Circumstantial evidence has also been offered in support of the possibility that at least one group of orchid genera has had a long involvement in shoot parasitism (Johansson, 1977). This author has suggested that the abbreviated shoot of *Microcoelia* Lindl. and other similar genera, like the

vestigial leaves of some unequivocal shoot parasites (e.g., *Cuscuta* L.), is indicative of an extended history of heterotrophy made possible by the acquisition of photoassimilates from an autotrophic host.

While this suggestion has some appeal, there is at least one other plausible explanation for the "shootless" condition in Orchidaceae that also has a nutritional basis, but not in parasitism. Rootlessness in *Tillandsia* L., an opposing but otherwise parallel condition that clearly has no relationship to hetertrophy, represents but one of many adaptations that have evolved in heterotrophy, to allow the more oliotrophic members of this genus to cope with the environmental restraints that select for high economy in mineral use and high fecundity in exposed portions of the epiphytic biotope (Benzing, 1978; Benzing & Davidson, 1979; Benzing et at., unpublished MS). The most important of these restraints are habitat infertility and the scattered location and ephemeral nature of suitable anchorage sites for heliophilic epiphytes in the forest canopy (Benzing, 1978). Shifts of function — in the case of Bromeliaceae, of salt and water absorption to the shoot — permits an economy in mineral expenditure unachievable by organisms with more conventional root systems (lower shoot-root ratios).

The shootless condition may exist in Orchidaceae to similar advantage. Many epiphytic orchids inhabit the same nutrient-stressed, unstable, patchy habitats occupied by the most specialized oligotropic bromeliads. By combining the functions of photoassimilation and water and salt absorption in the green roots in this case, scarce mineral nutrients ordinarily committed to more extensive developments of stems and leaves are available for allocation to the sexual effort and ultimately to an enhancement of fecundity and the ability to recruit adult replacements on emerging "patches" in a strongly *r*-selecting habitat.

One final point is in order. Epiphytic orchids lack haustorial roots, so that if parasitism does occur, a fungal intermediary must be present. The involvement of mycorrhizal fungi in any capacity during the adult life of epiphytic orchids remains to be demonstrated. No attempt was made by Ruinen (1953) to demonstrate the significance of hyphae in her material. My own limited observations (unpublished) and those of several others (Dycus, 1957; Sanford & Adanlawo, 1973) did not reveal the presence of fungal hyphae, pathogenic or symbiotic, in the roots of any of the epiphytic orchids examined, so that the relationship observed by Ruinen, whatever its nature, is not widespread. Until direct evidence is presented that mycorrhizal fungi can facilitate an orchid epiparasitism, we must assume that *Microcoelia* and its kind are, as extensive horticultural experience suggests of epiphytic orchids in general, fully capable of an autotropic existence, and that this is the practice they follow in nature.

LITERATURE CITED

Benzing, D. H. 1978. The life history profile of *Tillandsia circinnata* Schlecht. (Bromeliaceae) and the rarity of extreme epiphytism among the angiosperms. Selbyana 2: 325-337.

Benzing, D. H. & E. Davidson 1979. Oliogotrophic *Tillandsia circinnata* Schlecht. (Bromeliaceae): an assessment of its patterns of mineral allocation and reproduction. Amer. J. Bot. 66 (4): 386-397.

Benzing, D. H. & J. Seemann 1978. Nutritional piracy and host decline: a new perspective on the epiphyte-host relationship. Selbyana 2:133-148.

Cook, M. T. 1926. Epiphytic orchids, a serious pest on citrus trees. J. Dept. Agric. Puerto Rico 10(2): 5-9.

Dycus, A. M. & L. Knudson 1957. The role of the velamen of the aerial roots of orchids. Bot. Gaz. (Crawfordsville) 119: 78-87.

Halle', F., R. A. A. Oldeman & P. B. Tomlinson 1978. Tropical trees and forests. Springer-Verlag, New York.

Horn, H. S. 1971. The adaptive geometry of trees. Princeton Univ. Press, Princeton, New Jersey.

Johansson, D. R. 1977. Epiphytic orchids as parasites of their host trees. Amer. Orchid Soc. Bulletin 46: 703-707.

Nuernbergk, E. L. 1974. Die Bedeutung der Epiphytose nach Ruinen und anderer Faktoren für die Biologie epiphytischer Orchideen. Die Orchidee 25: 282-288.

Ruinen J. 1953. Epiphytosis. A second view on epiphytism. Ann. Bogoriensis 1 (2): 101-157.

Sanford, W. W. & I. Adanlawo 1973. Velamen and exodermis characters of West African epiphytic orchids in relation to taxonomic grouping and habitat tolerance. Bot. J. Linn. Soc. 66: 307-321.

Zimmerman, M. H. & C. L. Brown 1971. Trees: structure and function. Springer-Verlag, New York.